A NEW MIDDLE TERTIARY CROCODILE FROM LAKE PALANKARINNA, SOUTH AUSTRALIA

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Australosuchus clarkae is a new generalised Oligo-Miocene crocodilian from Lake Palankarinna, South Australia. It appears to be part of a recently recognised endemic Tertiary radiation of crocodiles in Australia.

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In another paper (Willis, Murray & Megirian 1990), the existence of an endemic Tertiary radiation of Gondwanan freshwater crocodilians in Australia was discussed. This speculation was based on zoogeographic considerations and apparently synapomorphic features possessed by *Pallimnarchus pollens, Quinkana fortirostrum* and *Baru darrowi.*

A new genus and species of crocodile from Oligo-Miocene sediments of South Australia appears to support this hypothesis. It is both the oldest described member of the group and, apparently, the most plesiomorphic. This species was noted by Molnar (1982) and probably by Stirton *et al.* (1968) and Estes (1984).

The following abbreviations for collections are used in this paper: AMNH, American Museum of Natural History, New York; NHMV P, Museum of Victoria, Melbourne; QM F, Queensland Museum, Brisbane; UCMP, University of California, Museum of Paleontology, Berkeley; SAM P, South Australian Museum, Adelaide.

SYSTEMATICS

Order: Crocodilia
Suborder: Eusuchia
Family: Crocodylidae
Australosuchus Willis & Molnar, gen. nov.

Type species

Australosuchus clarkae Willis & Molnar, sp. nov. (Figs 1a, b)

Generic diagnosis

Crocodiles of this genus differ from all other crocodylids in the following combination of features (apomorphies designated 'a'): moderately broad snouted; pseudoheterodont dentition; alveolar process present on premaxilla, maxilla and dentary; external nares raised, circular or ovate, with sharply defined margins; postorbital-squamosal contact on skull roof V-shaped, apex directed posteriorly (a); five alveoli occur in premaxilla; fourteen alveoli occur in maxilla; sixteen to seventeen alveoli occur in dentary; dentary tooth reception pits are excluded from margins of premaxilla and maxilla; fourth dentary tooth reception pit is semi-enclosed (a); symphysis extends posteriorly to level of fourth or fifth dentary alveolus.

Differential diagnosis and discussion

Australosuchus clarkae differs from other Australian crocodiles in the following features: *A. clarkae* lacks interlocking dentition, an anterior process of the palatines and has the fourth dentary tooth accommodated in a pit rather than a notch as in species of *Crocodylus.* The first of these features is apparently plesiomorphic for crocodiles, the second is probably apomorphic for certain Australian crocodiles (Willis *et al.* 1990), and the third is also found in alligatorines. As discussed below, *Australosuchus* seems to have no other alligatorine affinities, and so this feature is probably convergent and an apomorphy for *Australosuchus. Australosuchus* does not have ziphodont features as seen in *Quinkana fortirostrum* and it is smaller than both *Baru darrowi* and *Pallimnarchus pollens. Australosuchus clarkae* is also distinguished from these three fossil crocodilians by the fourth dentary tooth reception pit, the extent of the dentary symphysis and the more posterior position of the palatal fenestrae (a plesiomorphic feature). In these features, *A. clarkae* is sufficiently different to justify the erection of a new genus.

Etymology

The generic name is derived from the Latin *australis* meaning southern and *suchus* meaning crocodile. The gender is masculine.

Australosuchus clarkae Willis & Molnar, sp. nov.

Holotype

QM F16788 (Fig. 1a, b), an almost complete skull and mandible, incomplete cervical and dorsal vertebrae, scapula, humerus and dermal armour, collected by Michael Archer in 1975.

Type locality

An unnamed site from the base of the eastern end of the bluff that yielded the Tedford Local Fauna and Tedford East Local Fauna, Lake Palankarinna, South Australia.

Paratypes

NHMV P188441, right premaxilla and maxilla; SAM P27932, premaxillary fragment; SAM P27847, maxillary fragment; SAM P27933, maxillary fragment; NHMV P188437, right maxillary fragments; QM F18102, jugal; SAM P29580, jugal; NHMV P188439, right jugal; NHMV P188440, right jugal fragment; SAM P27841, frontals; SAM P10892, frontals; AMNH 23047, left postorbital and half of frontal; QM F17985, frontal, parietal and postorbital; AMNH 23048, right postorbital; AMNH 23049, parietal; AMNH 23052, right quadrate; AMNH 23051, left quadrate and squamosal fragment; QM F17433, right quadrate; QM F17986, squamosal (possibly from the same individual as QM F17985); QM F17984, squamosal; AMNH 23050, basioccipital; NHMV P166441, right exoccipital; QM F17983, exoccipital with quadrate fragment; SAM P27934, dentary, angular and squamosal; SAM P27827, dentary; SAM P29083, dentary; SAM P23985, dentary; NHMV P166439, right dentary; NHMV P160360 and NHMV P160357, right dentary fragment (two fragments of the same specimen that have been catalogued separately); NHMV P166442, left dentary; SAM P30162, right dentary; UCMP 57071, right dentary; UCMP 70941, left dentary; QM F18152, right dentary; QM F18151, left dentary; UCMP 100028, surangular; SAM P23985, surangular; NHMV P188436a, right surangular; NHMV P188438, right surangular; QM F17988, incomplete angular; SAM P23985, angular; SAM P29578, angular; SAM P29579, angular; NHMV P188436b, left angular fragment; AMNH 23055, cervical vertebral

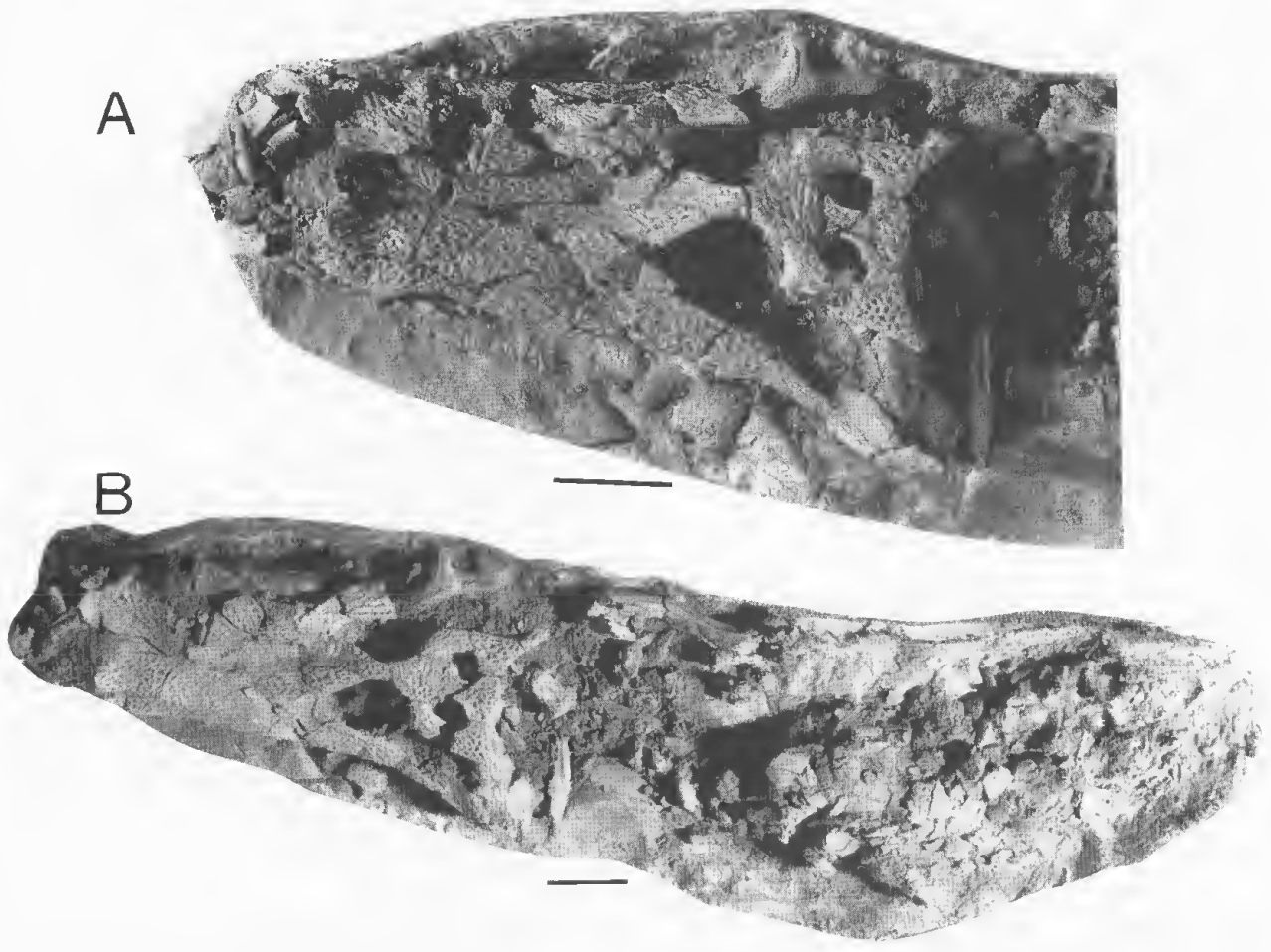


FIGURE 1. The type specimen (QM F16788), in its plaster cradle, of *Australosuchus clarkae*, gen. et sp. nov., in dorsal view. A, Skull. B, Entire specimen. Scale bars 5 cm.

centrum; SAM P27829, cervical vertebral centrum; AMNH 23056, neural arch; AMNH 23057, caudal vertebral centrum and neural arch; QM F17987, dorsal vertebra; AMNH 23054, cervical rib; SAM P24656, a right hind limb consisting of femur, tibia, fibula, a partial third tarsal, all metatarsals, one phalange and claw from the first digit, three phalanges and claw from the third digit and two phalanges from the fourth digit; SAM P30161, right femur; SAM P27830, right coracoid; SAM P27828, right third metatarsal; SAM P30160, right humerus; all from the Etadunna Formation, Lake Palankarinna, South Australia.

Paratype material from other localities includes: AMNH 12177, premaxilla and two teeth and AMNH 12200, a skull, both from the Namba formation, Lake Pinpa; NHMV P188442, right angular fragment from the Namba formation, Lake Tarkarooloo; UCMP 88192, jugal and quadratojugal and UCMP 71396, left premaxilla and maxilla both from the Wipijiri formation, Lake Ngapakaldi; UCMP 100027, frontals, UCMP 57069, dentary and UCMP 57071, dentary all from the Mampuwordu Sands, Lake Palankarinna.

AMNH 12200 is a large skull that is badly shattered (Fig 2). It can be referred to this species but is too poorly preserved to be of much descriptive value.

There are numerous other crocodilian fragments from Lake Palankarinna in the collections of the South Australian Museum and the Queensland Museum. These specimens are too small or broken to be of use. However, a search through these fragments revealed no specimens that clearly differed from those described here.

Various unnumbered specimens from the collections of the Queensland Museum and the South Australian Museum are also of use and are included here as paratypes.

Stratigraphy, fauna and age

The holotype derives from the Etadunna Formation. It belongs to an undetermined local fauna that is some two metres below the Tedford East Local Fauna and at a level that is stratigraphically comparable to the occurrence of *Muramura williamsi* (Pledge 1987; Archer, pers. comm.). This local fauna is most likely to be late Oligocene to early Miocene in age (Callen *et al.* 1987; Archer *et al.* 1990).

Paratype specimens from the Etadunna Formation belong to the Ditjimanka Fauna. AMNH 12200 and AMNH 12177 pertain to the Pinpa Local Fauna. NHMV P188442 belongs within the Lake Tarkarooloo Local Fauna. UCMP 88192 and UCMP 71396 belong to the the Kutjamarpu Fauna. Current understanding of the biostratigraphy places these faunas within the late Oligocene or early Miocene (Callen *et al.* 1987, Woodburne *et al.* 1985).

UCMP 100027, UCMP 57069 and UCMP 57071 are from the Mampuwordu Sands, Lake Palankarinna. The Mampuwordu Sands are thought to be late Pliocene or possibly early Pleistocene in age (Callen *et al.* 1987, Woodburne *et al.* 1985). Either this species of crocodile was conservative in its morphology over this period of time or the site information for these three specimens is incorrect. Considering that the Mampuwordu Sands are a channel cut into the Etadunna Formation, it is possible that these Mampuwordu crocodile specimens were reworked from the older Etadunna Formation or that their stratigraphic province was incorrectly interpreted at the time of collection. At present, we assume the site information for the supposed Mampuwordu Sands specimens is incorrect. Thus we suggest this species is most likely restricted to the late Oligocene or early Miocene.

Etymology

The specific name is in honor of Mrs Elaine Clark in recognition of her continuing support for the Riversleigh Research Project.

Specific diagnosis

As for the genus until new species are recognised.

Descriptions

The following descriptions are primarily based on the holotype, the most complete specimen. The paratypes were used to supplement this information because many elements on QM F16788 are incomplete, badly fractured or covered by matrix. Paratypes are noted where used. Fig 3 shows reconstructions of the skull, based on specimens shown in Fig. 4.

QM F16788 was chosen as the holotype for two reasons: it retains most of the skull elements and, although crushed and fractured, its skull could be reasonably well reconstructed; second, it is the only specimen that unambiguously associates cranial and postcranial elements.

Premaxillae: The premaxillae on QM F16788 are broken and incomplete so this description is based mainly on SAM P27932, AMNH 12177, NHMV P188441 and UCMP 71396 (Fig 5).

The external nares are raised. They are circular and slightly flared on SAM P27932, but on UCMP 71396 the nares are ovate, being wider than long. On both specimens the nares have sharply defined margins.

AMNH 12177 has two unattached teeth associated with it. They are ovate in cross section, with non-serrate anterior and posterior carinae. The larger has vertical ribs on the lingual surface. These

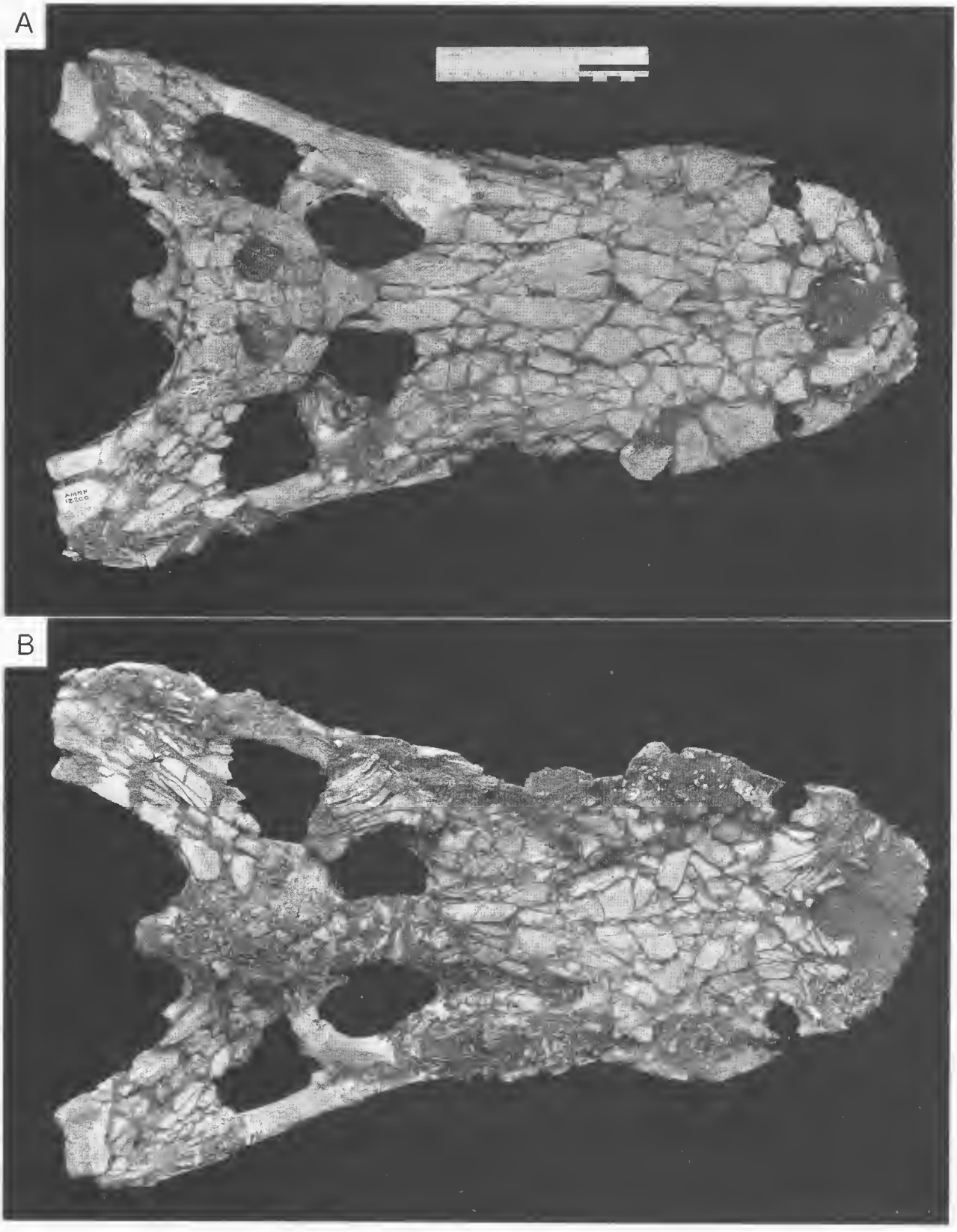


FIGURE 2. Large crocodilian skull (AMNH 12200) from the Namba Fm. of Lake Pinpa, South Australia. A, Dorsal view. B, Ventral view. This somewhat crushed specimen is probably referable to *A. clarkae*. Scale in inches and cm.

are the only teeth associated with any of the premaxillae.

There are five alveoli. The first and second are subequal in size, the third is larger and the fourth is very large. The fifth is intermediate in size between the second and third.

Dentary tooth reception niches occur between, and lingual to, the upper series and are excluded from the margins. The first niche is very deep and separates the first and second premaxillary alveoli. It does not erupt through the dorsal surface on SAM P27932 but does on UCMP 71396. The other niches are more shallow. The fourth dentary tooth reception pit is semi-enclosed, mostly hiding the fourth dentary tooth when the mouth is closed and thus resembling the alligatorine, rather than the crocodyline, condition. This is an unusual and distinctive feature. The premaxilla is built up around the tooth bases to form a distinct alveolar process. The sculpture consists of distinct oval pits around the margins and indistinct pits on the dorsal surface. The foramen incisivum is relatively large and ovate.

AMNH 12200 shows that the premaxillae are separated by the nasals on the dorsal surface, posterior to the nares, a feature not clear in any other specimen.

Maxillae: The maxillae of QM F16788 are almost complete but crushed and broken. The ventral surfaces are obscured by matrix and mandibular elements. The maxilla of UCMP 71396 is complete and uncrushed. NHMV P18841, NHMV P188437, SAM P27933 and SAM P27847 are less complete maxillary fragments. This description is based on these specimens.

The shape of the maxilla indicates a moderately broad and flat snout with fourteen alveoli. A moderately developed alveolar process is present, accommodating the anterior six alveoli.

No crowns are associated with any maxilla, except that of the type, where the left fourth and fifth are present. These are oval in section with marked anterior and posterior carinae. The alveoli are round, becoming ovate posteriorly. The sequence of tooth size is typically crocodyline (as judged by the size of the alveoli) with the fifth tooth being the largest. The alveoli increase in size from the first to the fifth then decrease in size to the seventh. They then increase in size again until the tenth and then decrease in size posteriorly. The third and tenth alveoli are about the same size but larger than the second, sixth, eighth and fourteenth alveoli which are also about the same size. The alveolar spacing is interrupted by dentary tooth reception pits between and lingual to the sixth and seventh alveoli, and between and lingual to the seventh and eighth alveoli.

Tooth reception pits are excluded from the margins and indicate that the teeth did not fully interlock. Well defined tooth reception pits are located between and lingual to the sixth and seventh alveoli, the seventh and eighth alveoli, the eighth and ninth alveoli and between the ninth and tenth alveoli. Less well defined pits occur between the first and second alveoli and posterior to the tenth.

The palatal suture with the premaxilla is a shallow W-shape and there is no clear sign of a contact with the palatine. However, the mid-line maxillary suture can be seen to extend posteriorly to the level of the anterior margins on the palatal fenestrae. This indicates that this species lacked an anterior palatal process. The ectopterygoid suture reaches anteriorly to the posterior edge of the twelfth alveolus. The palatal fenestrae reach anteriorly to the level of the ninth alveolus. The dorsal sutural contact with the nasal is nearly straight and almost parallel to the midline, but slightly constricted anteriorly.

Sculpture is shallow on the maxilla, consisting of low surface markings, pits anteriorly and grooves posteriorly.

Nasals: Both nasals on QM F16788 are crushed and broken. While no other specimens preserve the nasals, some inferences about these bones can be drawn from UCMP 71296 (premaxilla and maxilla), AMNH 12200 (a skull) and from UCMP 100027, (frontals and prefrontals).

The nasals entered the external nares, flared slightly toward the posterior until their contact with the lacrymals, then tapered posterior from that point. An anterior process of the frontals separated the posterior extremities of the nasals.

Jugals: The jugals of the type specimen are crushed and broken and the right has fallen away from the remainder of the skull so that the medial face is exposed. This description is also based on UCMP 88192, NHMV P188440, NHMV P188439 and SAM P29580 (Fig. 6a–d).

The jugals are slender and gracile. The postorbital bar is inset but there is no trough between it and the lateral face of the jugal. The postorbital bar has a weakly developed buttress on the medial surface that ventrally is deflected sharply forward. A very large nutrient foramen lies on the medial surface, anterior to the base of the postorbital bar. On UCMP 88192 and the type, there are two foramina here. The sculptured surface of the jugal extends ventrally under the region of the postorbital bar.

Quadratojugals: The quadratojugals on QM F16788 are broken and partially displaced. An almost complete quadratojugal is present in UCMP 88192. It is broad and ventrally thickened. The presence or absence of an anterior spike cannot be determined. Only subdued sculpture is present, and the ventral portion of the lateral face, behind the jugal contact, is flexed to be directed ventrolaterally.

Quadrates: The right quadrate of QM F16788 is

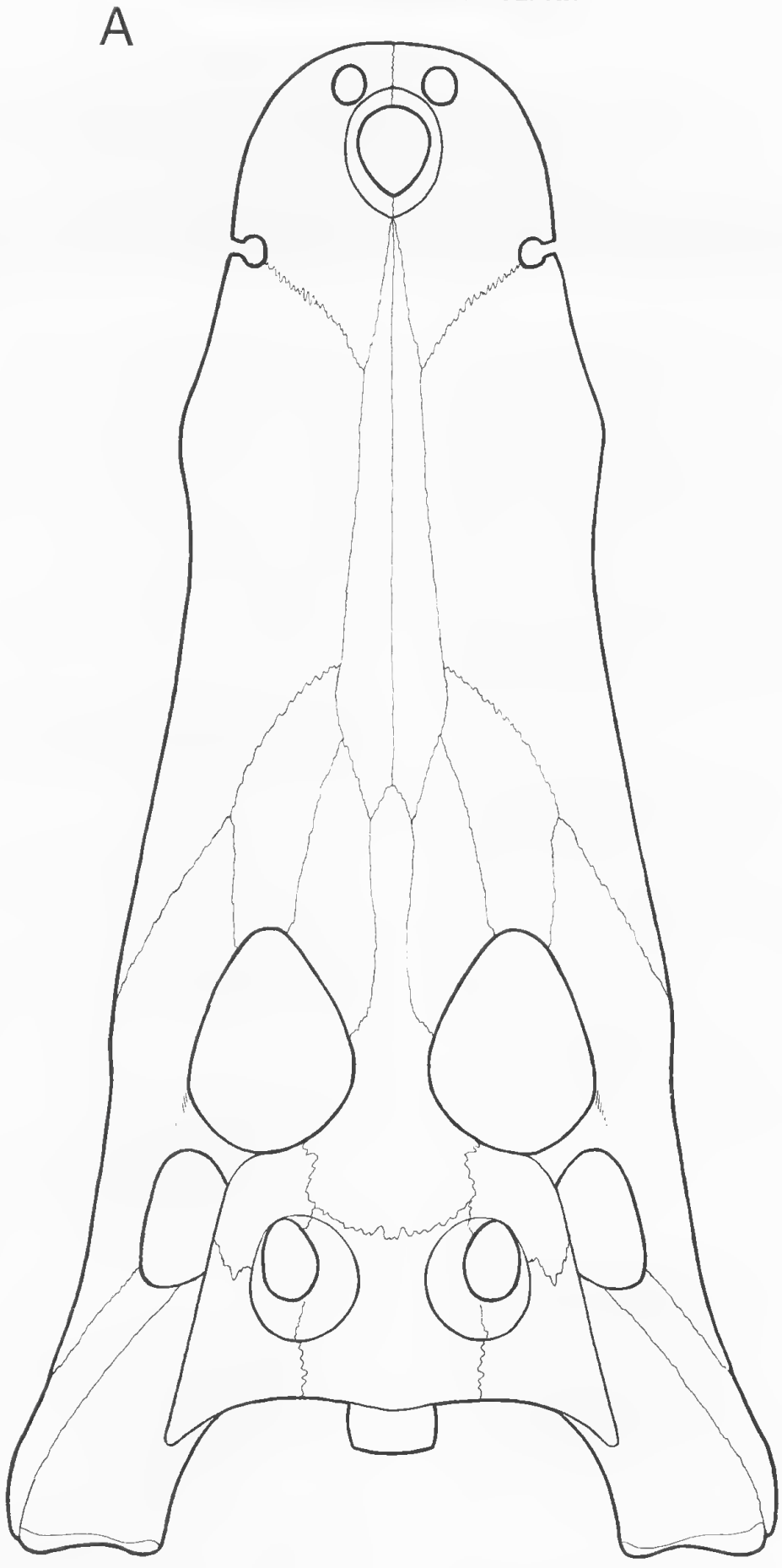
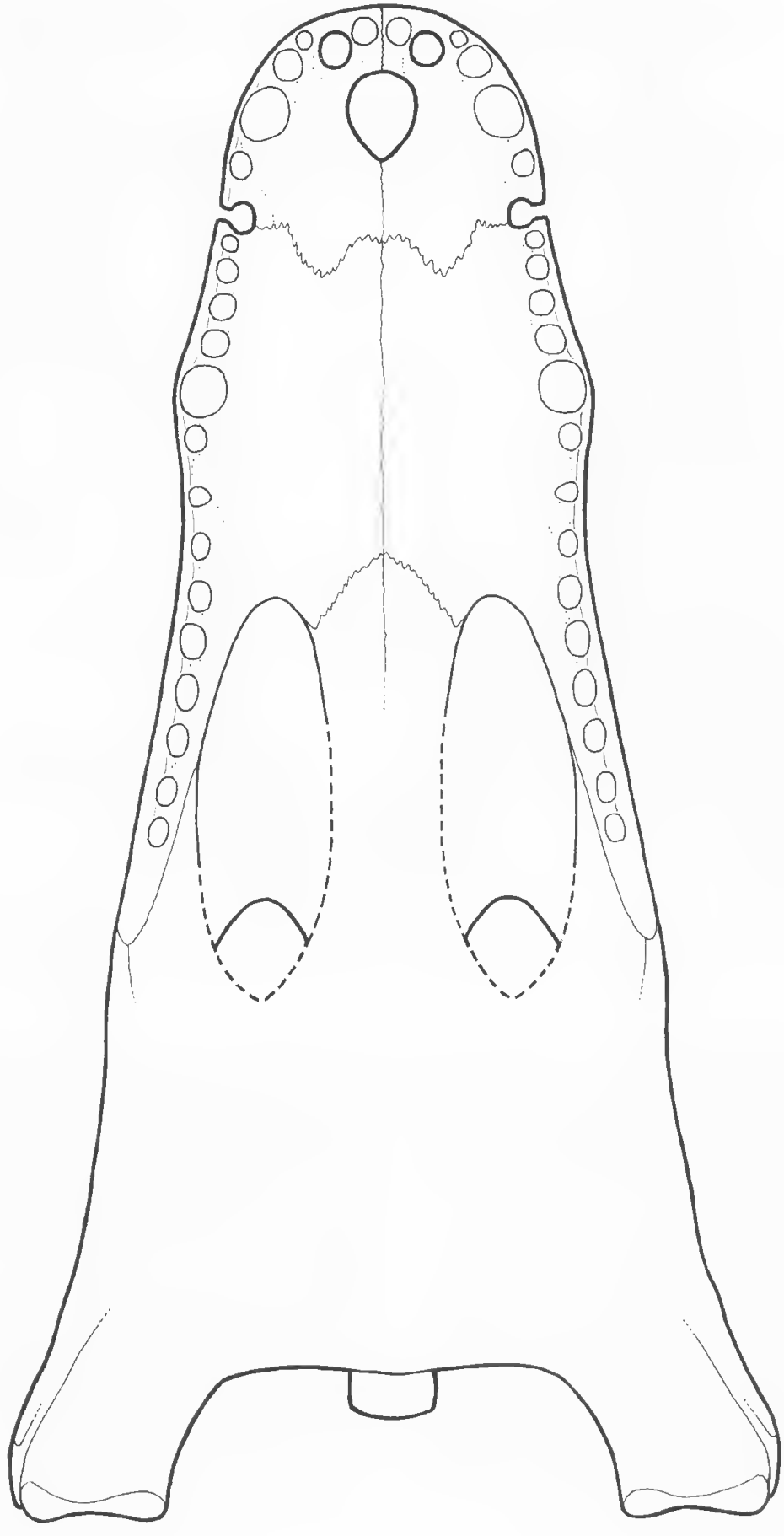


FIGURE 3. Reconstruction of the skull of *A. clarkae* in dorsal (A) and ventral (B) views. The posterior part of the palatal surface is unknown.

B



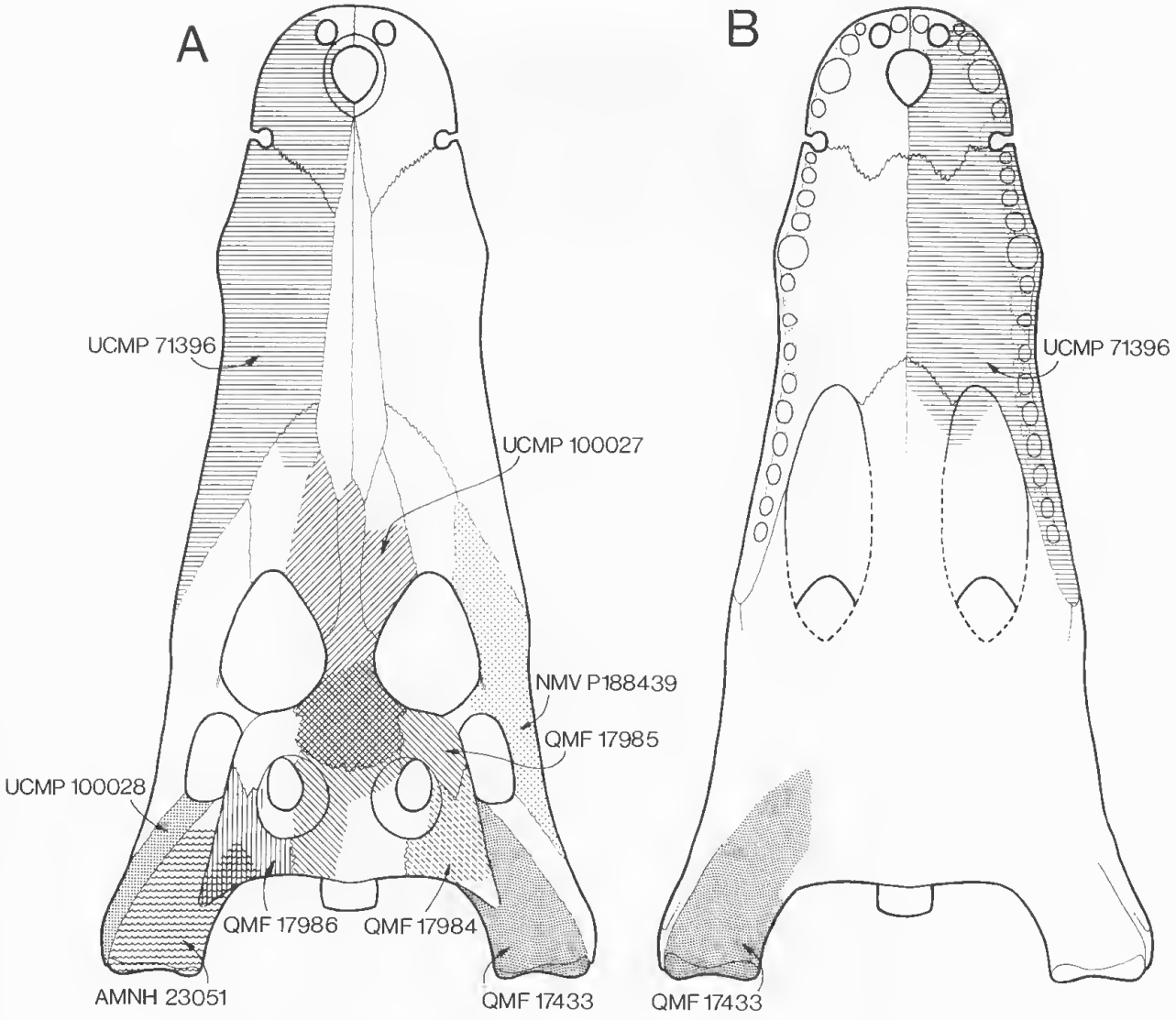


FIGURE 4. Specimens upon which the cranial reconstruction is based. A, Dorsal view. B, Ventral view.

missing and the left quadrate is broken and somewhat obscured by other elements. AMNH 23052 a right quadrate, AMNH 23051 a left quadrate and squamosal, and three unnumbered specimens (two right, one left, all missing the anterior portions) in the collections of the Queensland Museum form the basis of the description (Fig. 7)

The dorsal contact with the squamosal has a prominent plinth. A well developed crest on the ventral surface (equivalent to the B crest of Iordansky (1973)) is orientated parallel to the quadratojugal suture. Posteriorly this crest curves laterally, toward the quadratojugal suture which it meets just anterior to the condyle (Iordansky's B' crest). The sutured margin with the quadratojugal is quite deep posterior to the level of the paroccipital process, becoming more shallow anteriorly. The dorsal platform between the condyle and the paroccipital process is quite wide. A distinct, almost pit-like, excavation on the ventral face lies just anterolateral to the medial condyle.

Lacrymals: Both lacrymals on QM F16788 are crushed and broken but complete. The only lacrymal material known from the paratype collection is a small fragment attached to UCMP 71396.

The lacrymals are relatively long and narrow. They form the antero-lateral margin of the orbits which are large and constricted anteriorly. They have an extensive medial contact with the nasals. The lacrymal duct and ventral surfaces cannot be traced in these specimens.

Prefrontals: The right prefrontal of QM F16788 is severely broken, but the left has suffered only one break near its centre and is apparently complete.

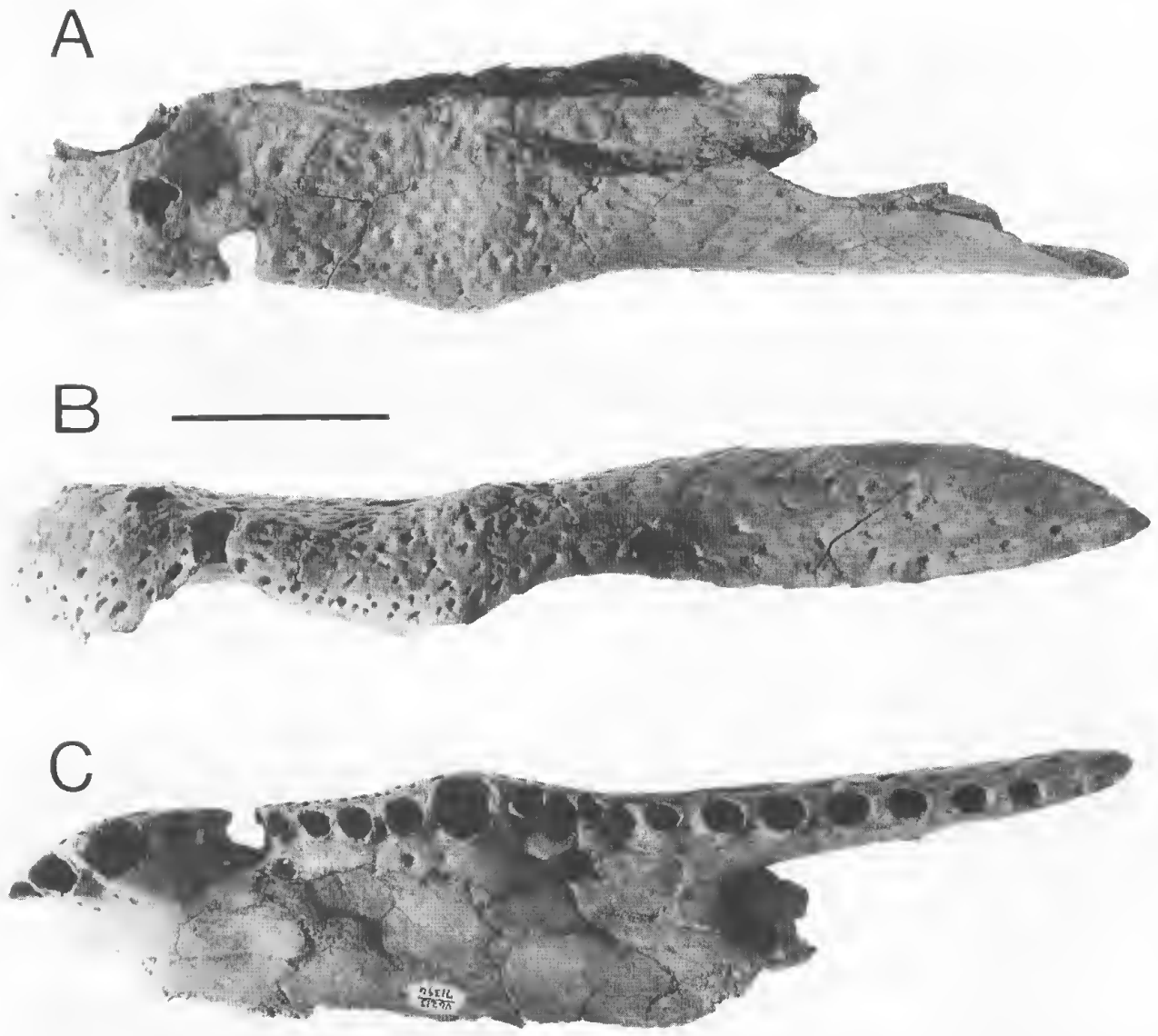


FIGURE 5. The left premaxilla and attached maxilla of *A. clarkae* (UCMP 71396) in dorsal (A), lateral (B) and ventral (C) views. Scale bar 5 cm.

UCMP 100027 preserves both left and right prefrontals; the right is incomplete anteriorly and both lack the delicate descending process.

The prefrontals are basically isosceles triangles with the apex directed laterally. The anterior process is relatively long and the posterior extremity of the nasals separates the anterior tip of the frontals from the prefrontals. Although the orbit margins are not raised, they are sharply defined and steeply angled to the external surfaces. There is a slight continuation of the *cristae cranii frontales* onto the posterior part of the ventral surface of the prefrontals. Sculpture consists of deep elongate pits.

Frontals: The frontals of QM F16788 are broken in one place. SAM P27841 and SAM P10892 are complete frontals, UCMP 100027 are complete frontals with prefrontals and part of the nasals (Fig. 6e, f) and AMNH 23047 is half a left frontal and a postorbital. All are similar but AMNH 23047 is smaller than the others.

The frontals of this species are slightly concave posteriorly due to raised orbital rims. They are heavily built (particularly posteriorly), narrow between orbits and lightly sculptured with pits. The anterior process is relatively long and anteriorly separates the posterior extremities of the nasals. Ventral ridges around orbits (*crista cranii frontales*) are not as well developed as in *C. porosus* of similar size, but in AMNH 23047 they are more pronounced than in the other specimens. The frontals do not participate in the margins of the supratemporal fenestrae. The dorsal suture with the

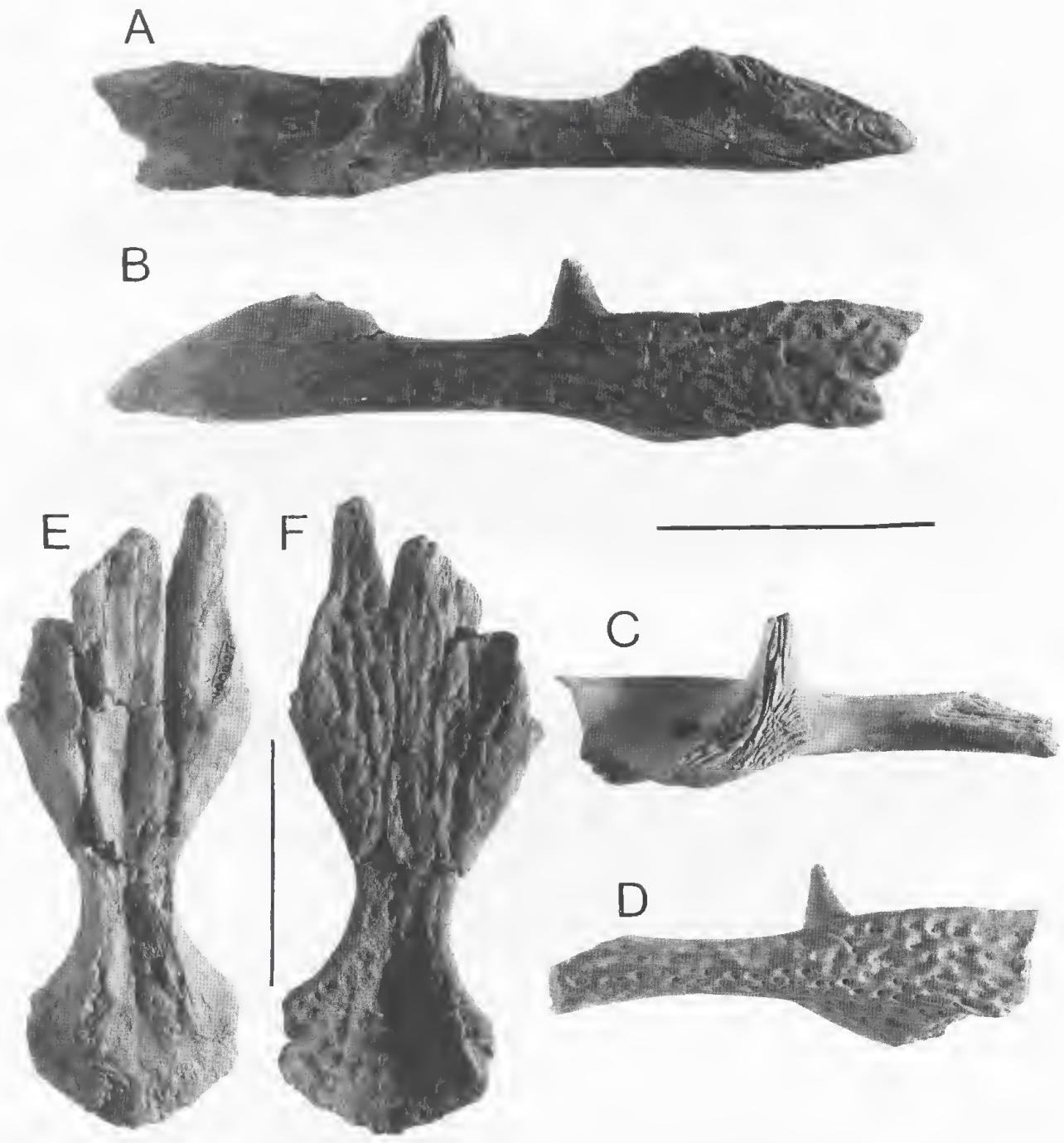


FIGURE 6. The right jugal with attached quadratojugal of *A. clarkae* (UCMP 88192) in medial (A) and lateral (B) views. The right jugal (QM F18102) in medial (C) and lateral (D) views. The frontals (UCMP 100027) in ventral (E) and dorsal (F) views. Scale bars 5 cm.

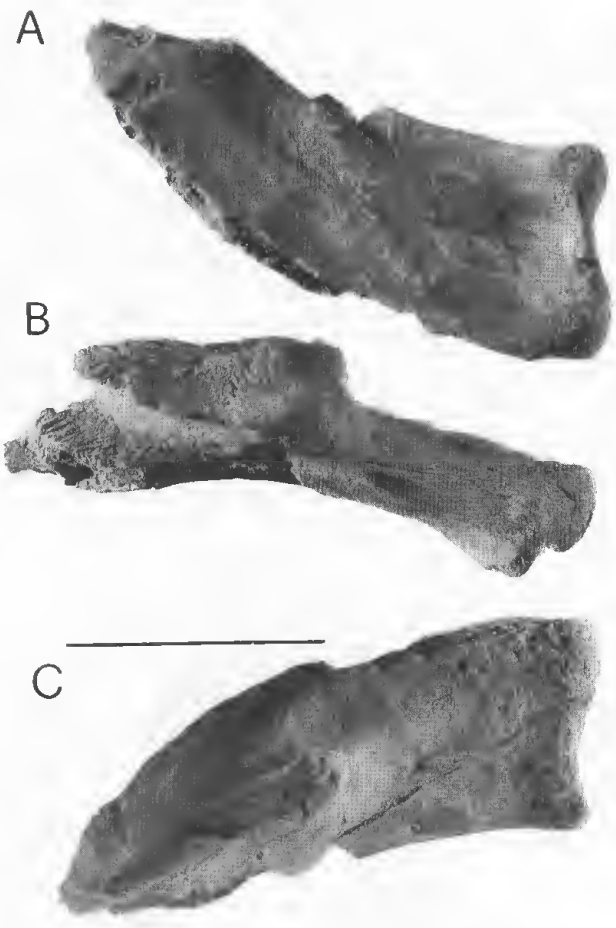


FIGURE 7. The right quadrate of *A. clarkae* (QM F17433) in ventral (A), medial (B) and dorsal (C) views. Scale bar 5 cm.

postorbital is directed medially then posteriorly in some specimens (UCMP 100027 and some unnumbered specimens in the Queensland Museum) but not in others (*e.g.* QM F16788).

Parietals: The parietals are preserved on QM F16788 but are broken between the supratemporal fenestrae. AMNH 23049 is a complete parietal, QM F17985 is a frontal, parietal and postorbital, and there are unnumbered parietals in the collection of the South Australian Museum.

The dorsal surface of this element is shallowly concave, posteriorly rising to the dorsal margins of the supratemporal fenestrae. The supratemporal fenestrae are large and round and the parietals are constricted between them. Anteriorly, the parietals send a thin lateral process to the postorbital, separating the frontals from the supratemporal fenestrae. There is a well-developed transverse bar on the ventral surface in the region of the diencephalon.

Postorbitals: QM F16788 has both postorbitals preserved, but both have the postorbital bar broken and the left is posteriorly incomplete. AMNH 23047 is a left postorbital and half frontal, QM F17985 is a frontal, parietal and postorbital, and AMNH 23048 is a right postorbital.

The postorbital is flat on the dorsal surface and relatively thick. There is a deep nutrient foramen on the anterolateral edge, at the top of the postorbital bar. QM F17985 shows a posterior process on the dorsal surface that overlaps the squamosal, separating the lateral and medial sides of its anterior extremity.

Squamosals: Both squamosals are preserved in QM F16788. AMNH 23051 is a left squamosal fragment attached to a quadrate. QM F17986 is a squamosal (possibly from the same individual as QM F17985) and QM F17984 is also a squamosal.

This relatively thick element is flat on the dorsal surface, forms the posterolateral margins of the supratemporal fenestrae and has a well-defined lateral edge forming the dorsal margin of the temporal arcade. This edge has a ventral lip. The anterior process extends under the postorbital. The squamosal extends further ventrally on the posterior wall of the skull than in *C. porosus* and the posterolateral crest of the squamosal is better developed than on *C. porosus* and continuous. The posterior face of the squamosal is concave.

Basioccipital: On QM F16788 the basioccipital is obscured. AMNH 23050 is a basioccipital. There is one unnumbered basioccipital in the UCMP collection, assumed to represent this species because of its locality and similarity to QM F16788 and AMNH 23050.

This element is narrower and extends further ventrally than in *C. porosus.* There is a deep eustachian foramen ventrally and a well-developed medial ridge on the ventral part of the posterior wall. Unlike *C. porosus,* the eustachian foramen is not enclosed by the basioccipital; the posterior half of the eustachian foramen is bounded by the basioccipital. The occipital condyle is set on a prominent neck, that projects further than in *C. porosus.*

Exoccipitals: Only the posterior wall of the exoccipitals of QM F16788 are visible. These are broken and partially obscured. NHMV P166441 is a right exoccipital. The ventral portion of QM F17983 is an exoccipital including the base of the paraoccipital process to the foramen magnum.

The positions of the foramina for cranial nerves X, XI and XII are as in *C. porosus.* The broken ventral face reveals the passage for the posterior carotid, and the broken dorsal surface exposes the internal chambers of the exoccipital that occupy the bulk of this element. The posterior face is more strongly convex than in *C. porosus* and the posterior opening of the cranio-quadrate passage is very close to the ventral margin.

Other skull elements: Palatines, vomers, basisphenoids, laterosphenoids, pterygoids and ectopterygoids have not been identified. They are all presumably present on QM F16788 but may be obscured by matrix and other bones.

Dentaries: The anterodorsal portion of the left dentary is present in QM F16788 but it is badly broken. The right dentary is possibly present but covered by matrix. Paratypes SAM P27934, SAM P27827, SAM P29083, SAM P23985, SAM P30162, NHMV P166439, NHMV P160360 (and NHMV P160357), NHMV P16644, UCMP 57071, UCMP 70941, QM F18151, QM F18152 and unnumbered specimens in the collection of the Queensland Museum are all dentaries (Figs 8 and 9).

The dentary is moderately broad and pseudoheterodont with an alveolar process that varies in development according to tooth size and extends back to at least the fourteenth alveolus. Pseudoheterodonty and the development of the alveolar process may be related to ontogeny because these features are not as strongly developed in small (presumably younger) specimens. The dentary body deepens posteriorly from the level of the fifteenth alveolus.

SAM P29083 and SAM P23985 display sixteen alveoli but QM F18152 displays seventeen in the right dentary. The teeth are arranged in a typically crocodyline sequence of enlargement. The first and fourth alveoli are the largest. The second, third and

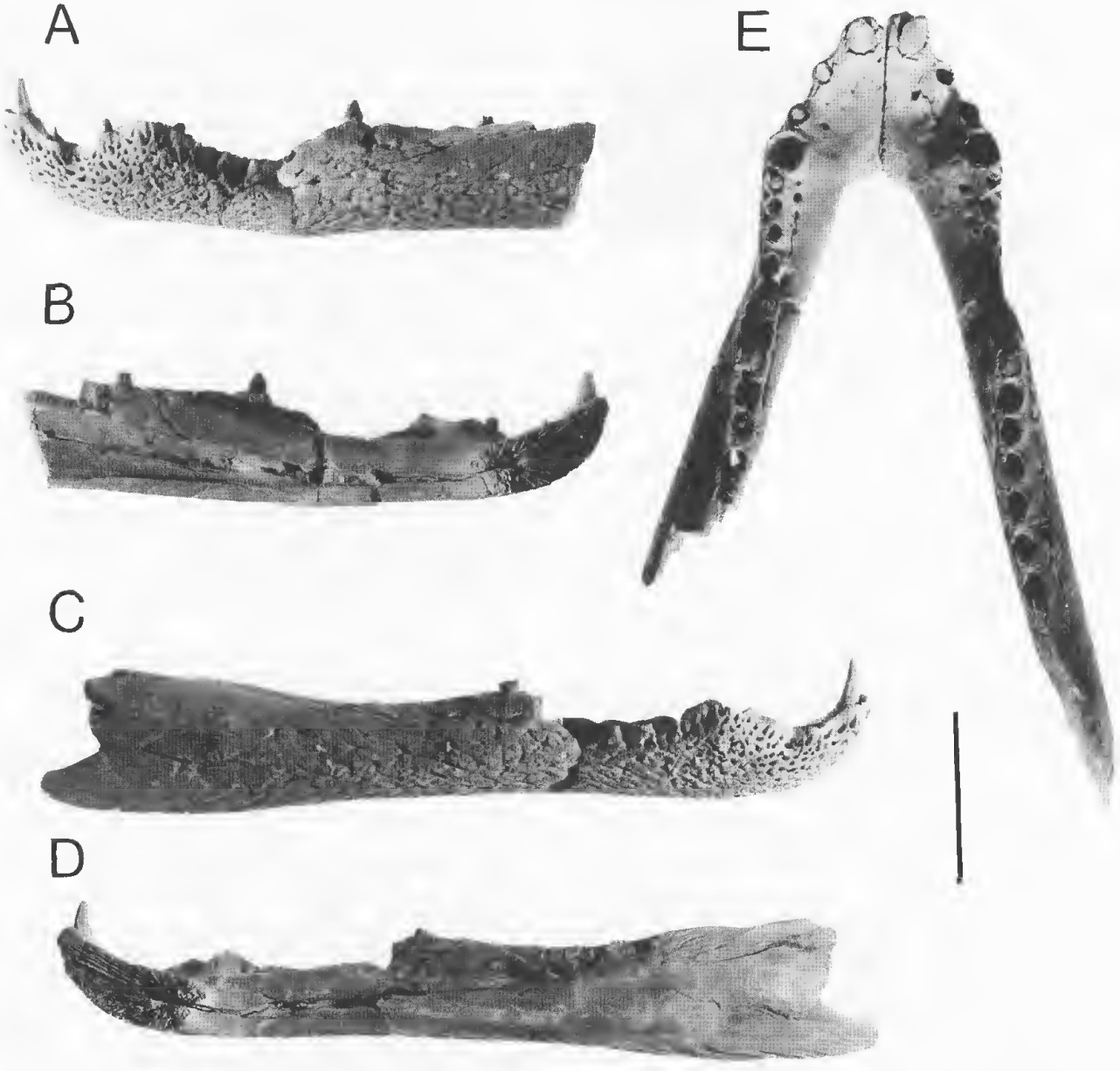


FIGURE 8. The dentaries of *A. clarkae*. A, Left dentary (QM F18151) in lateral, and B, medial view. C, Right dentary (QM F18152) in lateral, and D, medial view. E, Both dentaries articulated in dorsal view. Scale bar 5 cm.

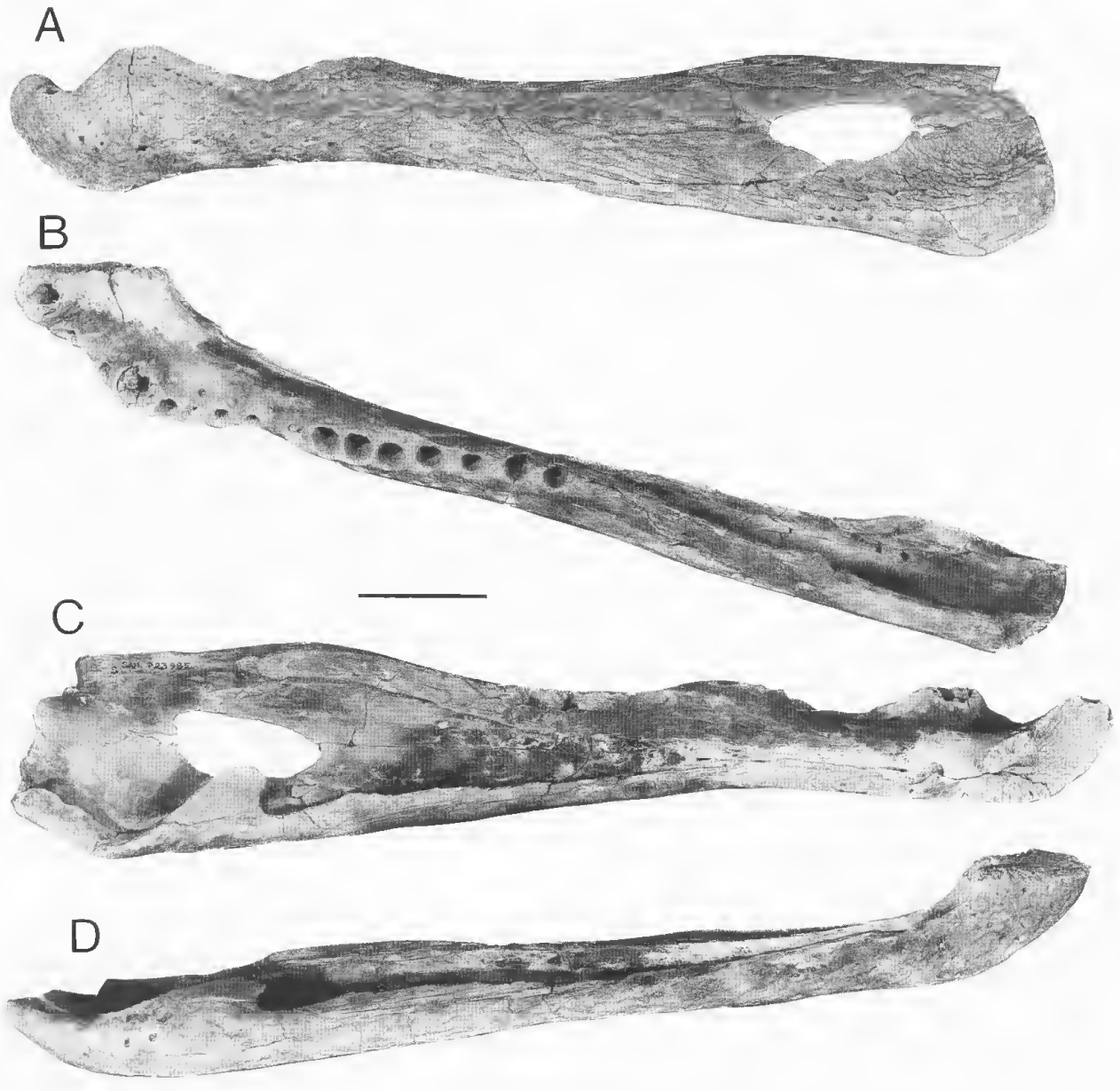


FIGURE 9. Left dentary with articulated angular and surangular (SAM P23985) of *A. clarkae*. A, Lateral view. B, Dorsal view. C, Medial view. D, Ventral view. Scale bar 5 cm.

the fifth through to the tenth teeth are all similar and smaller in size. The teeth posterior to and including the eleventh are similar in size and intermediate between the size of the smaller and larger teeth in the anterior of the dentary. The anterior alveoli are round but posterior alveoli are ovate. SAM P30162 is a more robust dentary and the fourth dentary alveolus is greatly enlarged. This has forced the third and fifth alveoli more toward the medial than in the other dentaries.

There is a deep indentation between, and buccal to, the second and third alveoli to receive the fourth premaxillary tooth. Other such indentations are located between and buccal to the first and second, fifth and sixth, sixth and seventh, seventh and eighth, and eight and ninth alveoli.

The symphysis extends posteriorly to the fourth alveolus in some (UCMP) specimens and the fifth alveolus in others. The splenial extends to the level of the seventh alveolus in some specimens and the eighth alveolus in others but this feature cannot be seen in all specimens. The symphyseal region is broad and upswept anteriorly. It is markedly broader than in *C. porosus* of comparable size.

Sculpture is of small point-like pits anteriorly and posteriorly, with sulci extending posteriorly from

these pits. A distinct row of dorsally opening buccal foramina occurs parallel to the margin of the dentary from the medial side of the first alveolus to the seventh alveolus.

The first, second, third, fifth, eleventh and thirteenth crowns are present in QM F18151 and the fifteenth is present but broken. The first crown is slender, recurved and almost D-shaped in section, with mesial and distal carinae. The posterior face is longitudinally striate. In section the first crown is wider that it is long, being about two-thirds as long (anteroposteriorly) as broad (mesiodistally).

Of the second, third and fifth crowns, only the tips are visible but they appear to be laterally compressed with mesial and distal carinae.

The eleventh crown is blunt, but laterally compressed with mesial and distal carinae.

Surangulars: Neither of the surangulars of QM F16788 are clearly visible. Paratypes SAM P23985, NHMV P188438 and NHMV P188436a are surangulars. The surangular of this species does not appear to differ greatly from those of other crocodilians although it is slightly more gracile than normal.

Angulars: The angulars of QM F16788, if present, are obscured by matrix. Paratypes SAM P23985, SAM P29578, SAM P29579, NHMV P188442, QM F17988 and NHMV P188436b are all angulars.

The angulars, although basically similar to each other in general form, show a surprising amount of variation in detail. The longitudinal ridge on the floor of the internal, ventral canal may be well developed and prominent (as in SAM P23985 and SAM P23578) or low and poorly developed (as in SAM P29579). SAM P29578 has only one large foramen in the ventral canal whereas SAM P23985 and SAM P29579 have two small foramina. SAM P29578 has a flared rim extending from the posterior side of the internal ascending (coronoid) process flaring medially and extending posteriorly to the posterior ascending margin. This flared rim is not seen in the other specimens. However, these are minor differences and, considering the variation seen in comparing specimens of other crocodilians, there is no reason to suspect that these angulars do not represent the same species.

Other mandibular elements: The articulars, coronoids and splenials may be present on QM F16788 but if so are obscured by matrix. These elements were not identified among the paratypes.

Mandibular fenestrae: Both the external mandibular fenestrae and the inferior internal fenestrae are best preserved in SAM P23985.

The external mandibular fenestra is quite large for a crocodyline. It is subtriangular. The 'hypotenuse' forms the superior border, which is inclined to the ventral margin of the mandible.

The inferior internal foramen is only known from its ventral and posterior margins. These give the impression of a relatively large size for this foramen.

Postcranials: Although there are many postcranial elements associated with the holotype and paratypes, these are not described in detail here. Most are poorly preserved or do not differ significantly from comparative specimens of *C. porosus* and *C. johnstoni*. However, the following observations may be made with confidence: 1, all vertebrae apparently are procoelous; 2, cervical vertebrae (AMNH 23055) are strongly keeled; 3, dorsal arches (centra eroded prior to collection) are best preserved, lacking only the dorsal spine, and the prezygopophyseal facets are not laterally extended as in *C. porosus* (Fig. 10); 4, cervical arches are broken but resemble those of *C. porosus* (Fig. 11); 5, the humerus is broken and the articular ends are missing, but it agrees in proportions with that of *C. porosus*; 6, the coracoid and the preserved portion of the scapula visible are no different from those of *C. porosus*; 7, The numerous scutes have no keel and a sculpture of pits that are not as deep as those on the skull (Fig. 12); 8, long elements of the limbs (humerus, femur, tibia, fibula and metatarsals) are straighter than in either *C. porosus* or *C. johnstoni* but otherwise similar; 9, the vestigial fifth metatarsal is much more robust and thick than the corresponding element in other crocodilians.

Phylogenetic Affinities

At present, a phylogenetic systematic analysis of the affinities of *A. clarkae* is considered premature. Such an analysis will be more meaningfully conducted within the context of a broader examination of all Australian and non-Australian crocodilians, many of which are presently under study. Consequently the affinities of *A. clarkae* are here outlined in only a cursory manner.

The position of the choanae cannot be seen on any of the specimens. However, the basioccipital AMNH 23050 is notched on the ventral side of the anterior process to accommodate the narial passage. This indicates that the internal nares must have been situated posteriorly in the palate. This feature, together with the presence of procoelous vertebrae and the subdermal postorbital bar indicate that this is an advanced eusuchian crocodylid (Steel 1973). Although the semi-enclosed fourth mandibular tooth could suggest alligatorine affinities, the contact of the nasal and the lacrymal (seen in *Alligator* and some fossil alligatorines), the sequence of maxillary tooth enlargement (the fifth being the largest rather than the fourth, an alligatorine apomorphic character-state) and the general form of the skull indicate crocodyline

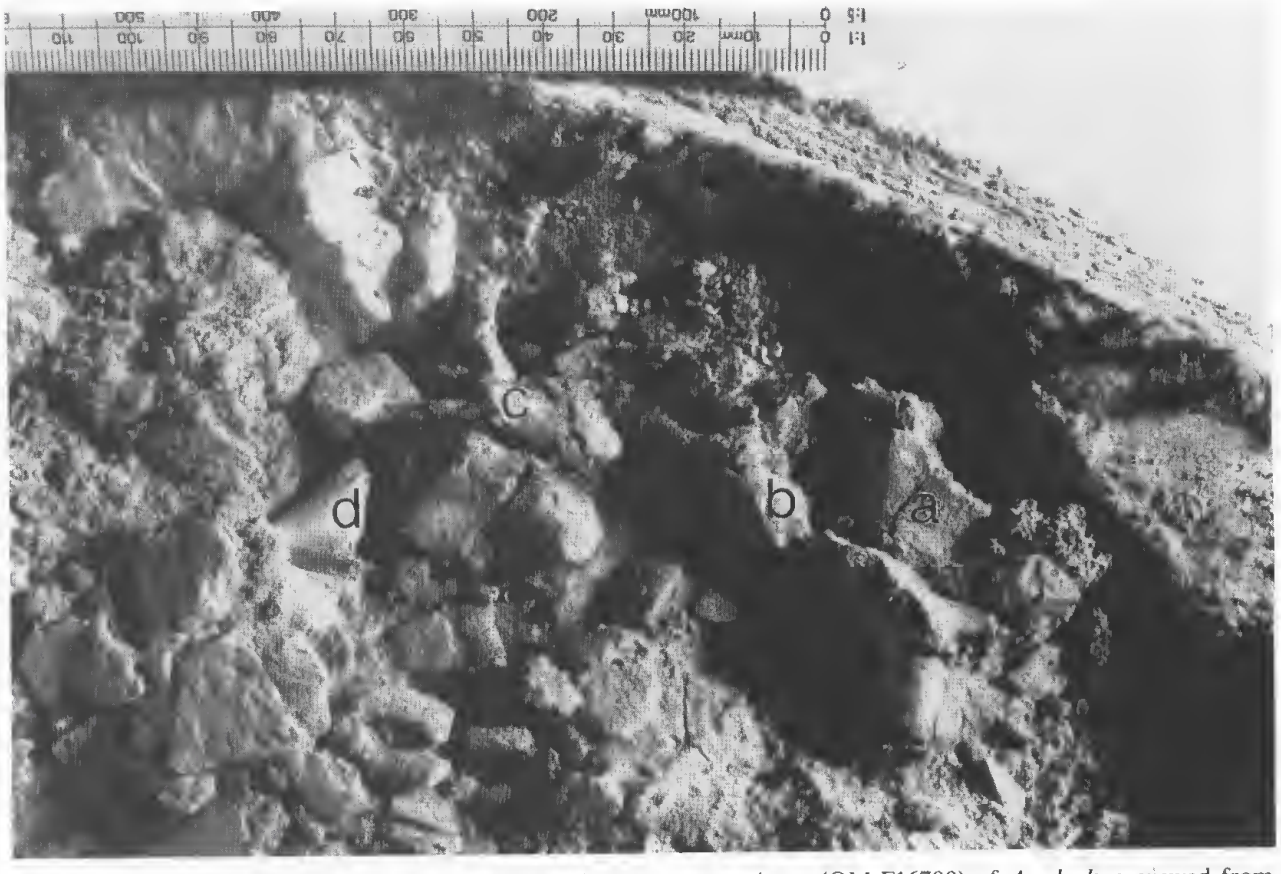


FIGURE 10. The dorsal neural arches as preserved in the type specimen (QM F16788) of *A. clarkae*, viewed from above. a, Nearly complete arch. b, c, d, Fragmentary arches (d in posterior aspect). Scale in mm.

FIGURE 11. The cervical vertebrae and scapula, as preserved, in the type specimen (QM F16788) of *A. clarkae*, in lateral view. c, Centrum (viewed obliquely from above). p, Prezygapophyses. pa, Parapophysis. s, Scapula. Scale in mm.

FIGURE 12. Dorsal osteoderms, *in situ,* of the type specimen (QM F16788) of *A. clarkae,* in dorsal view. Two complete osteoderms are indicated by arrows just at left of centre and at bottom-centre. Scale in mm.

affinities. Thus the semi-enclosed fourth mandibular tooth is probably a convergent feature.

Australosuchus clarkae shows some features that have been tentatively proposed as synapomorphies of an Australian Tertiary crocodile radiation (Willis *et al.* 1990). These include the lack of an anterior process of the palatine, the degree and sequence of tooth enlargement in the dentary and the presence of an overbite. The lesser development of an alveolar process on the premaxilla and maxilla and the palatal fenestrae being more posteriorly located than in other Australian crocodilians suggest that *A. clarkae* is a more plesiomorphic member of this group.

There is a striking resemblance between the anterior portion of the dentaries of *A. clarkae* and *B. darrowi* which suggests a close affinity between the two. However, they differ in the posterior extent of the mandibular symphysis. In *Baru* the symphysis extends to the level of the sixth or seventh alveolus while in *Australosuchus* it extends only to the level of the fourth or fifth alveolus.

Discussion

Australosuchus clarkae is a freshwater crocodilian of moderate size from the late Oligocene and early Miocene of central Australia. To date, it is the oldest described member of the Australian Tertiary radiation of crocodiles (Willis *et al.* 1990). It shows some features that suggest it may be the most plesiomorphic member of this group. *Australosuchus clarkae* is considered to be a generalised crocodilian, that is, it lacks features commonly associated with more specialised crocodilians such as longirostrine, ziphodont or brevirostrine characters.

As discussed briefly above, the Mampuwordu specimens obstensibly represent this species in late Pliocene or early Pleistocene time in the Lake Palankarinna area. However, cataloguing or collecting errors may be involved. While the possibility that this species remained largely unchanged from the late Oligocene to the Pleistocene could not be ruled out, such extreme morphological conservatism seems unlikely even in situations where environments persisted for long times. Unfortunately, without considerably more research, details of preservation cannot be reliably used to distinguish between specimens of the Mampuwordu deposit and those from the older Etadunna deposits (Archer, pers. comm.)

Material belonging to *A. clarkae* has been mentioned by other authors. Estes (1984)

commented that the only crocodilian material in a sample of fossils from Lake Palankarinna were small, unidentifiable teeth. Stirton *et al.* (1968) mentioned unidentifiable crocodilian remains from Lake Palankarinna. Molnar (1982) briefly mentioned the 'Etadunna' crocodilian suggesting that it may be related to a crocodilian from Murgon in south-east Queensland. Because there is no evidence of more than one crocodilian from Lake Palankarinna in the extensive collections of material examined in this study, it seems reasonable that crocodilian material mentioned by these authors can be attributed, at least tentatively, to *A. clarkae*.

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